Insect-oak Interactions with Coast Live Oak (*Quercus agrifolia*) and Engelmann Oak (*Q. engelmannii*) at the Acorn and Seedling Stage[1]

Connell E. Dunning,[2] Timothy D. Paine,[3] and Richard A. Redak[3]

Abstract

We determined the impact of insects on both acorns and seedlings of coast live oak (*Quercus agrifolia* Nee) and Engelmann oak (*Quercus engelmannii* E. Greene). Our goals were to (1) identify insects feeding on acorns and levels of insect damage, and (2) measure performance and preference of a generalist leaf-feeding insect herbivore, the migratory grasshopper (*Melanoplus sanguinipes* [Fabricus] Orthoptera: Acrididae), on both species of oak seedlings. Acorn collections and insect emergence traps under mature *Q. agrifolia* and *Q. engelmannii* revealed that 62 percent of all ground-collected acorns had some level of insect damage, with *Q. engelmannii* receiving significantly more damage. However, the amount of insect damage to individual acorns of both species was slight (<20 percent damage per acorn). *Curculio* occidentis (Casey) (Coleoptera: Curculionidae), *Cydia latiferreana* (Walsingham) (Lepidoptera: Tortricidae), and *Valentinia glandulella* Riley (Lepidoptera: Blastobasidae) were found feeding on both species of acorns. No-choice and choice seedling feeding trials were performed to determine grasshopper performance on the two species of oak seedlings. *Quercus agrifolia* seedlings and leaves received more damage than those of *Q. engelmannii* and provided a better diet, resulting in higher grasshopper biomass.

Introduction

The amount of oak habitat in many regions of North America is decreasing due to increased urban and agricultural development (Pavlik and others 1991). In addition, some oak species are exhibiting low natural regeneration. Although the status of Engelmann oak (*Quercus engelmannii* E. Greene) natural regeneration has been confirmed in several studies (Muick and Bartolome 1986, Osborne 1989), the increased urbanization in these areas is cause for additional research that seeks to provide management methods to ensure the maintenance of Engelmann oak stands. Engelmann oak is a species of concern in California due its limited distribution and occurrence in the growing urban areas surrounding Los Angeles and San Diego (Osborne 1989). Another oak species co-occurring with *Q. engelmannii* throughout most of its range, coast live oak (*Quercus agrifolia* Nee), also has exhibited reduced

---

[1] An abbreviated version of this paper was presented at the Fifth Symposium on Oak Woodlands: Oaks in California's Changing Landscape, October 22-25, 2001, San Diego, California.
[2] Environmental and Community Planner, Bureau of Land Management., Palm Springs-South Coast Field Office, 690 West Garnet Ave., P.O. Box 581260, North Palm Springs, CA 92258 (e-mail: connell@alumni.utexas.net)
[3] Professors, Department of Entomology, University of California, Riverside, CA 92521 (e-mail: timothy.paine@citrus.ucr.edu and redak@citrus.ucr.edu, respectively)

natural regeneration in central California (Muick and Bartolome 1986). A lack of natural regeneration of this oak has not been identified for southern California; however, coast live oak also occurs in areas currently experiencing increased pressure from urban and agricultural development. Because of reduced habitat and regeneration problems, the factors that may be limiting natural replacement of oaks are of interest to land managers. In particular, potential factors affecting the most vulnerable stages in the oak life cycle, including the acorn and seedling stage, may provide information that will aid in maintaining current oak stands.

For acorns, the impact that insect feeding may have on germination is not well understood and may vary among oak species. Previous research suggests that insect damage to acorns may be a cause for limited natural germination of oak (Korstian 1927, Marquis and others 1976, Oliver and Chapin 1984, Weckerly and others 1989). While there is evidence that damaged acorns are still able to germinate (Walters and Auchmoody 1993), insect infestation of acorns may limit seedling vigor (Gribko 1995). It is not known how insect damage to acorns affects long-term vigor of seedlings and saplings. Tecklin and McCreary (1991) found that a larger acorn mass was positively associated with increased survival and height of blue oak, *Quercus douglasii* Hook. & Arn. A decreased mass of acorn reserves as a result of insect herbivory may reduce necessary reserves for seedling growth (Andersson 1992, Oliver and Chapin 1984). Artificial herbivory experiments confirm this trend, as acorns with more of the cotyledon removed are unable to survive when nutrient reserves are reduced (Kaushal and others 1993).

Defoliation of seedlings by herbivores has been implicated in areas with poor restoration success and is a potential causal mechanism for lowered natural regeneration, especially by damaging young leaf tissue (Tecklin and others 1997). Seedlings are affected more severely by herbivory than older saplings and mature trees, because relatively low levels of defoliation are sufficient to kill a seedling or trigger morphological changes to seedling leaves that result in decreased vigor (Larson 1978, Moller 1995, Moller and de Lope 1998). Additionally, herbivore damage to young seedlings can be detrimental to subsequent growth in some species of trees (McClaran 1985).

The specific impact that insect herbivory may have on juvenile oaks is poorly understood, but insect herbivory may be a factor in limiting the recruitment of seedlings to saplings. Several species of canopy- and seedling-feeding lepidopterans exhibit periodic increases in population sizes and have been shown to reduce survival of oak seedlings (Shaw 1974). The most common insects found feeding on oak seedlings in natural and restoration settings are grasshoppers (Adams and others 1991, Griffin 1971, McCreary and Tecklin 1994, McPherson 1993), which have been implicated as a causal factor in the failure of oak restoration efforts (McCreary and Tecklin 1994). In some areas, grasshopper damage has been significant enough to require insect barriers to prevent massive seedling mortality (Adams and others 1987, McCreary and Tecklin 1994). While southern California oak savanna habitats support many species of grasshoppers, the generalist feeder, *Melanoplus sanguinipes* (Fabricus), represents up to 95 percent of all grasshoppers collected in summer months (Porter and Redak 1997). This grasshopper is likely the most prevalent insect herbivore throughout the year in southern California oak woodlands (Porter and Redak 1997), and has the potential to consume large quantities of foliage, especially during years when population sizes are large (Capinera and Sechrist 1982).

Here we summarize two studies. The objectives of the first study (Acorn Study) were to determine (1.1) what insects are found feeding on acorns of *Q. agrifolia* and *Q. engelmannii* and what level of insect damage is present; (1.2) what the location of the insect-caused damage is on the acorns of both species; and (1.3) what the level of multiple infestation occurs in individual acorns. The objectives of the second study (Seedling Study) were to determine (2.1) the performance (as estimated by consumption and growth) of the generalist grasshopper, *M. sanguinipes*, feeding upon *Q. agrifolia* or *Q. engelmannii* seedlings; (2.2) if this grasshopper species shows a preference for either oak species; and (2.3) if herbivory by this species significantly damages either *Q. agrifolia* or *Q. engelmannii* seedlings.

Methods

Acorn Study

Emergence Traps

In order to identify adult weevils emerging from the ground beneath mature *Q. agrifolia* and *Q. engelmannii* trees, seven emergence cone traps (Raney and Eikenbary 1969) were placed underneath Engelmann and coast live oak trees at Santa Rosa Plateau Ecological Reserve (SRPER; 10 kilometers northwest of Temecula, California). Traps were placed under individual mature oaks (1 per tree) at randomly chosen locations underneath the canopy and were not moved throughout the study. Traps were initially placed in the field on April 20, 1999 and checked monthly for emerging weevils between April and September 1999.

One-month Emergence Trial

To identify individual and multiple accounts of insects infesting acorns from both *Q. agrifolia* and *Q. engelmannii* and to correlate amount and location of damage with particular insect species, a sample of 730 acorns from the 1998 acorn crop was collected in January 1999. Acorns were collected from two locations: SRPER and Southwestern Riverside County Multispecies Reserve (SWRCMSR; 20 kilometers northeast of Temecula, California). Acorns were collected from the ground beneath eight *Q. engelmannii* (n=530 acorns) and nine *Q. agrifolia* (n=200 acorns). Each acorn was placed into an individual rearing vial. Acorns were checked daily for emergence of larvae and parasitoids for a period of one month after collection.

After allowing one month for larvae to emerge, percent desiccation was estimated for each acorn, and all acorns were dissected to determine additional live and dead insect inhabitants, levels of multiple infestation and percent and type of damage (identified by weevil or lepidopteran frass). A ranking of insect-caused damage was applied to each acorn using the following damage-ranking scale of 0 to 6 (after Swiecki and others 1990): 0= no damage visible, 1= trace to 2.5 percent, 2= >2.5 percent to 20 percent, 3= >20 percent to 50 percent, 4= >50 percent to 80 percent, 5= >80 percent to 97.5 percent, and 6= >97.5 percent.

Monthly Samples

In July 1999, a second experiment was initiated to collect samples throughout the growing season from the 1999 acorn crop. These samples were collected to compare temporal variation in insect infestations, to further identify acorn inhabitants, and to determine the extent and location of damage to acorns. Samples (>30 acorns per tree) were taken from five *Q. agrifolia* and five *Q. engelmannii* trees (lower canopy) each month from August 1999 until the end of acorn fall in December 2000. A subsample of 20 acorns per tree was dissected and damage was ranked as above for each monthly sample. Location of damage (apical/basal) was also determined for every acorn.

Seedling Study

Seedlings of *Q. engelmannii* and *Q. agrifolia* were acquired from a local nursery in May 1999 and maintained throughout the experiment in a greenhouse at the University of California, Riverside. Grasshoppers (*M. sanguinipes*) were collected from SRPER on July 7, July 14, and August 1, 1999 and held in group cages with a diet of half wheat germ:half oat bran, iceberg lettuce, and sprouts until experiments began.

No-choice Experiment

To determine grasshopper performance and potential damage to both species of oaks, 30 *Q. agrifolia* and 30 *Q. engelmannii* seedlings were measured for total leaf area, then caged individually. After an initial starvation period of 24 hours, fourth-instar grasshoppers were weighed and then caged on each of the 30 *Q. engelmannii* and *Q. agrifolia* oak seedlings. At the end of the 20-day feeding period, all grasshoppers were removed and their fresh mass determined. Grasshoppers were then dried and weighed and all frass produced by each grasshopper during the trial was collected, dried, and subsequently weighed. Biomass gain of each grasshopper was estimated by subtracting initial dry masses from final dry masses. Grasshopper performance was measured by comparing final dry mass and biomass gain. We also compared the grasshoppers' utilization of both species of oaks. To determine the amount of grasshopper damage to both species of oak seedlings, amount of leaf biomass consumed was measured.

Choice Experiment

In order to determine grasshopper preference for either species, 20 pairs of *Q. engelmannii* and *Q. agrifolia* seedlings were measured for leaf area, and each pair placed into double acetate feeding chambers as above. Twenty grasshoppers were placed individually into feeding chambers containing a pair of oak seedlings. Extent of feeding damage was determined after 14 days by measuring the amount of leaf area consumed (original leaf area minus remaining leaf area). To determine if grasshopper preference was greater for either *Q. agrifolia* of *Q. engelmannii* seedlings, amount of leaf biomass removed was compared between the two species.

Results

Acorn Study

Identification of Acorn Inhabitants—All Collection Methods

The weevils collected from both the emergence trial and the monthly acorn samples were all larvae in the genus *Curculio*. None of the weevils collected from acorns became adults during the course of this research; consequently, identification to species was not possible; however; all adult weevils found in traps placed below mature trees were identified as *Curculio occidentis* (Casey) (Gibson 1969). Two species of lepidopteran larvae and adults found from the emergence trial and from the monthly samples were *Cydia latiferreana* (Walsingham) (Lepidoptera: Tortricidae) and *Valentinia glandulella* Riley (Lepidoptera: Blastobasidae). Several species of parasitoids were found throughout the study *(table 1)*. No cases of weevil parasitism were found in either species of oak acorns.

Table 1—*Parasitoids reared from Lepidoptera feeding on* Q. engelmannii *and* Q. agrifolia *acorns.*

Parasitoid	Host	Emergence date
Ichneumonidae		
Ctenopelmatinae (1)	*Q. engelmannii*	May 23
Pimplinae, (3)	*Q. agrifolia*	March 23
	Q. engelmannii	May 5
Braconidae		
Chelorinae, *Phanerotoma* sp. (1)	*Q. engelmannii*	March 15
Orgilinae, *Orgilus* sp. (2)	*Q. engelmannii*	January 14
Microgastrinae, *Dolichogenidea* sp. (1)	*Q. agrifolia*	April 16
Encyrtidae		
Copidosomatini, *Copidosoma evansi* (44)	*Q. engelmannii*	June 28

Emergence Traps

All weevils found in adult collection traps and on trees were identified as *Curculio occidentis.* Two weevil ovipositions were observed during the study. One female *Curculio occidentis* was observed ovipositing onto a *Q. agrifolia* acorn on October 14, 1999 and a second female was observed ovipositing onto an acorn of *Q. engelmannii* on October 29, 1999.

One-month Emergence Trial

Of the ground collected acorns, 62.3 percent exhibited some level of damage. Although the majority of all acorns were damaged, the level of damage was low (ranking of “1”= trace to 2.5 percent damage and “2”= >2.5 percent to 20 percent damage) for most acorns collected. A higher proportion of *Q. engelmannii* (58 percent) acorns were damaged than were *Q. agrifolia* (29 percent) acorns (χ^2= 46.8; $p<0.05$). A greater proportion of weevils, moth larvae and adults, and lepidopteran parasitoids were found within acorns of *Q. engelmannii* than in *Q. agrifolia.*

Insects emerged from 80 of 730 (11.0 percent) of the acorns collected. Of these, 117 weevil larvae emerged from 72 acorns, nine lepidopteran larvae emerged from nine acorns, and three additional lepidopteran larvae were parasitized. A total of eight out of 200 *Q. agrifolia* acorns in the rearing vials had insects emerge. After dissections, an additional 11 live weevils and 23 live lepidopteran larvae were found. Thirty-five dead weevils, seven dead lepidopteran larvae and 46 dead parasitoids (44 from one acorn) were found. A total of 111 acorns of *Q. engelmannii* contained weevils (21.0 percent of Engelmann acorns collected) and 41 acorns contained

Lepidoptera larvae and adults (7.7 percent); 39 *Q. agrifolia* acorns contained weevils. (19.5 percent of *Q. agrifolia* acorns collected), and only one *Q. agrifolia* acorn contained Lepidoptera larva (0.5 percent).

There were four co-occurrences of a *C. latiferreana* and a weevil within single *Q. engelmannii* acorns. No *Q. agrifolia* acorn sampled had both species inside. There were 68 occurrences of more than one *Curculio* sp. within a single *Q. engelmannii* acorn, and there were three occurrences of multiple *Curculio* sp. within single *Q. agrifolia* acorns *(fig. 1)*.

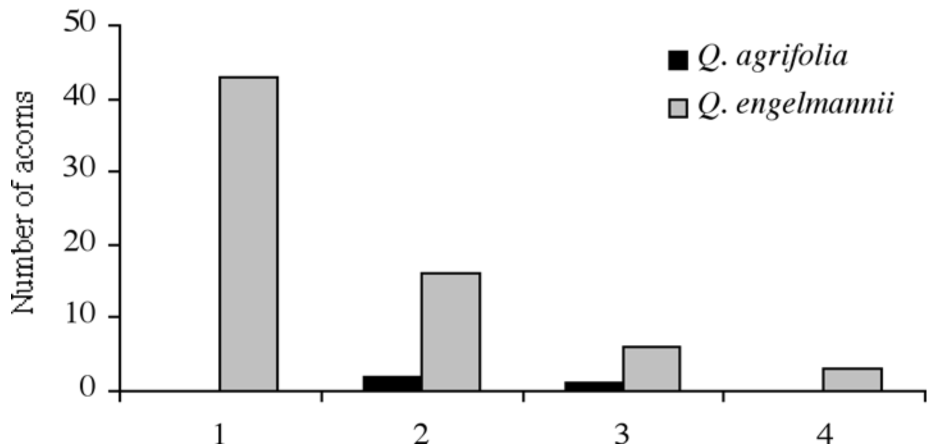

Figure 1—Number of acorns with different numbers of *Curculio* sp. weevils within a single acorn collected from ground samples in January 1999. Acorns collected were from the 1998 acorn crop.

Monthly Samples

In the subsequent July-December 1999 samples, overall damage to all acorns also was minimal (average damage rankings below 2), with no significant difference between the amount of damage found on subsampled *Q. agrifolia* and *Q. engelmannii* acorns (*t*-test; $t_{1,14}$= 1.4; p>0.05). The majority of damage to all acorns with over 50 percent damage was in the basal portion of the acorn for both oak species *(fig. 2)*, with, *Q. agrifolia* acorns exhibiting a higher proportion of basally damaged acorns (*t*-test; $t_{1,14}$= 3.2; p<0.05). The apical end of the acorn contains the growing embryo. There was no significant difference observed in the location of damage within Engelmann acorns (*t*-test; $t_{1,14}$= 1.4; p>0.05).

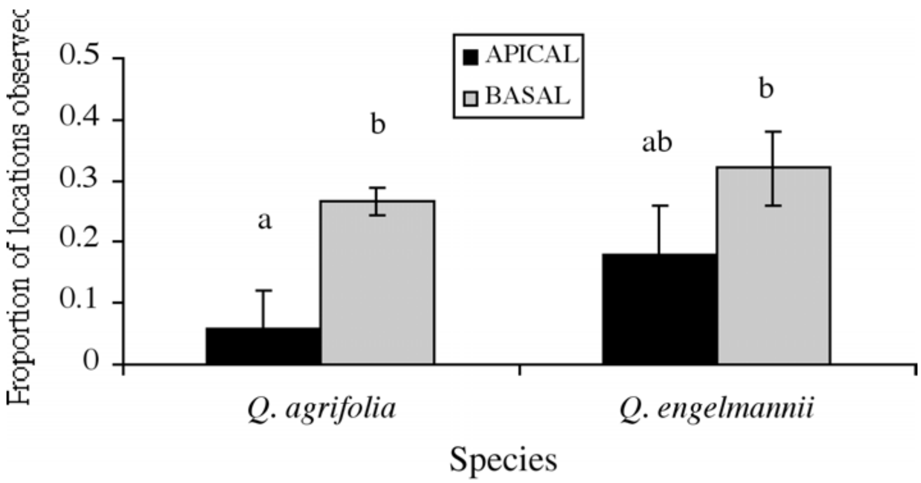

Figure 2—Proportion of *Quercus agrifolia* and *Q. engelmannii* acorns with apical and basal damage. Bars are means (±SE) for all acorns exhibiting over 50 percent damage from insects. Letters above bars indicate means are significantly different (t-test; *P*<0.05).

Numbers of oviposition scars peaked in late October 1999 for Engelmann acorns and August 1999 for coast live oak acorns. A significant amount of the variation in the number of weevil oviposition scars was described by the date of acorn collection for both *Q. agrifolia* ($F_{5,24}$= 5.4; p<0.01) and *Q. engelmannii* (*fig. 3*; $F_{5,24}$= 9.0; p<0.001). Date of collection also described a significant amount of the variation observed in insect damage for both species, with the amount of insect damage increasing seasonally ($F_{5,54}$= 9.6; p<0.001). The availability of acorns on each tree from which acorns were sampled (represented by a ranking of 0-6) was not a significant predictor of the number of weevil ovipositions observed for either species (Analysis of variance [ANOVA] for *Q. agrifolia*; $F_{5,24}$= 0.8; p>0.05; ANOVA for *Q. engelmannii*; $F_{3,26}$= 0.7; p>0.05).

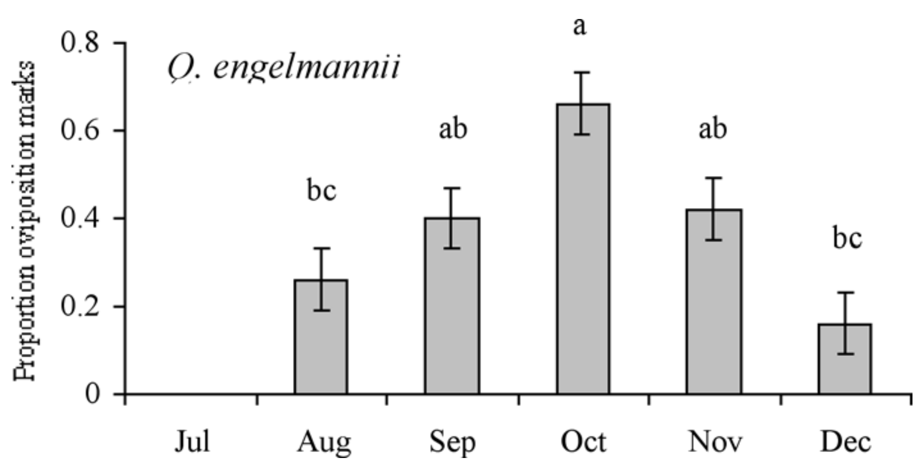

Figure 3—Average *Curculio* sp. oviposition marks per acorn found on acorns collected from *Quercus agrifolia* and *Q. engelmannii* in July through December 1999 samples. Values shown are least square means (±SE; n=5/month). Different letters above bars indicate means are significantly different among species (Ryan-Einot-Gabriel-Welsch multiple-range test ANOVA; P<0.05)

Seedling Study

No-choice Experiment: Grasshopper Performance

Grasshoppers feeding upon *Q. engelmannii* gained significantly less biomass than those feeding upon *Q. agrifolia* (Analysis of covariance [ANCOVA]; $F_{1,47}$= 18.6; p<0.001); in fact, they actually lost biomass over the course of the 20-day experiment. There was no significant interaction between initial biomass and the grasshopper biomass gained ($F_{1,46}$= 1.9; p>0.05).

Grasshoppers feeding on either oak species produced equivalent amounts of frass once the total amount consumed had been taken into account (ANCOVA; p>0.05). Analysis of covariance, with biomass consumed as a covariate, did not indicate a difference between tree species.

No-choice Experiment: Damage to Seedlings

Q. agrifolia seedlings in the feeding trials had more available leaf mass than the same age *Q. engelmannii* seedlings. Once effects of initial insect mass and availability of seedling biomass were removed, more *Q. agrifolia* seedling leaves were damaged than *Q. engelmannii* leaves (ANCOVA; p<0.001). Plant size was not a factor affecting herbivory. Grasshoppers preferred to feed upon *Q. agrifolia* seedlings, regardless of the available seedling biomass associated with each species of seedlings. As with the preceding analyses, there were no interaction effects between treatment and the covariate of initial plant mass ($F_{1,49}$= 2.0; p>0.05) or the covariate of initial grasshopper mass ($F_{1,49}$= 1.2; p>0.05).

Choice Experiment: Grasshopper Preference

After adjusting for the biomass of seedlings available for consumption, grasshoppers preferred to consume more *Q. agrifolia* biomass (ANCOVA; p<0.001). As in the no-choice trials, grasshoppers did not prefer to feed upon seedlings with greater biomass available (ANCOVA; p>0.05). There was no significant interaction between the biomass of seedlings initially available and the mass of leaves consumed by the grasshoppers ($F_{1,36}$= 2.9; p>0.05).

Discussion

Acorn Study

While the larvae were not confirmed to be *Curculio occidentis* and did not pupate during the course of the research, the occurrence of the adults of this species in the collection traps indicates that this species uses both *Q. agrifolia* and *Q. engelmannii* as a host and that the collected larvae are likely this species as well. The observation of females ovipositing on acorns of both oak species further confirms the association of *C. occidentis* with both species of oaks. *Curculio occidentis*, *C. latiferreana,* and *V. glandulella* are all listed in the most recent edition of the California Oak Disease and Arthropod (CODA) Database (Swiecki and others 1997a) and are cited as herbivores of *Q. agrifolia*. This study confirms their association with *Q. engelmannii* as well. The two moths, *Cydia latiferreana* and *V. glandulella*, are common among oak species, with the latter most commonly detected as a secondary pest feeding on acorns that have been previously damaged by *Curculio* sp. (Bonner and Vozzo 1987). *Valentinia glandulella* also has been found to feed on undamaged acorns (Galford 1986). In the current study, this species was both a primary herbivore (found feeding with no other previous damage observed) and a secondary herbivore (found feeding on previously damaged acorns).

The majority of acorns studied in the emergence trial were damaged; however, the total damage to each acorn was slight. During the one-month emergence trials, insects emerged from only 10 percent of all acorns collected. Despite the discovery of insects within acorns after dissections, the total number of insects found remained small. As all acorns in the emergence trial were collected from the ground in January, the level of insect damage observed and the number of insects collected represents a bias towards acorns not taken by vertebrates. Vertebrate herbivores were not excluded from the areas where acorns were collected. Thus, depending upon the acorn foraging preferences of vertebrates, the actual percentage of insect damaged acorns from the entire crop of acorns may be incorrectly estimated. In the subsequent monthly sampling period of acorns collected from the canopy, the extent of damage to each acorn examined matched the results found in the one-month emergence trial. There was no significant difference between the two species of oaks in damage incurred by insects.

Percentage of damaged acorns has been observed to be as high as 80 percent within one stand of oaks (Scutareanu and Roques 1993). In Marin county, northern California, Lewis (1991) found 25 percent of *Q. agrifolia* acorns sampled had signs of insect boring activity. Out of 501 acorns dissected, 38 percent had signs of insect damage; 70 percent were damaged by a *Curculio* sp. and 30 percent were damaged by the filbertworm. Swiecki and others (1991) found up to 47 percent of some *Q. douglasii* samples with *Curculio* sp. and 60 percent with *C. latiferreana*. We found 21 percent of ground-collected *Q. engelmannii* acorns contained *Curculio* sp. weevil larvae and 8 percent contained lepidopteran larvae. The number of ground-collected *Q. agrifolia* acorns containing weevil larvae was 20 percent and 0.05 percent contained lepidopteran larvae. Number of insects from this study are lower than numbers found in other studies; however, the number of damaged acorns was much higher and these numbers represent only ground-collected acorns from one season. Insect damage levels to oaks in California vary with yearly acorn production among and within trees from year to year (Koenig and others 2002). Acorn surveys at the Santa Rosa Plateau indicate that the 1998 acorn crop for Engelmann was high, while the acorn crop for coast live oak was fair. The 1999 acorn crop was determined to be better than average for coast live oak and a low acorn year for Engelmann oak. The year to year variation observed in acorn numbers may impact the numbers of infested acorns found. Because of the annual variability that exists in the numbers of acorns produced and the insects feeding on them, insects may have a significant impact on this oak system (Swiecki and others 1991).

The damage observed to the acorns resulted from larval tunneling throughout the acorn. Several of the acorns collected in this study showed no external signs of insect damage, yet had signs of insect tunneling beneath the pericarp. The majority of both ground-collected and canopy-collected acorns were significantly more damaged in the basal, or cap end, portion of the acorn than in the apical, growing end of the acorn; however, the proportion of damage that was apical was higher for *Q. engelmannii*. This has implications for the potential for Engelmann oak acorns to germinate after being partially damaged. If the apical, or growing embryo tip, of the acorn is damaged, then the potential for germination is reduced (Bonner and Vozzo

1987). Previous research has suggested that granivores preferentially feed upon the basal portion of acorns to avoid a higher tannin concentration in the growing tip (Steele and others 1993). Although no plant chemistry was described for either species in this study, the majority of damage seen was in the basal portion for both species.

Only 4 of 750 (0.5 percent) acorns in emergence trials contained more than one insect species feeding within the same acorn. *Cydia latiferreana* and a *Curculio* sp. were the two species found together within single acorns. Co-occurrence of both a *Cydia* sp. and a *Curculio* sp. larva within a single nut also has been observed in previous studies of oak and chestnut systems (Lewis 1991, 1992; Swiecki and others 1991; Debouzie and others 1993; Arahou 1994). Arahou (1994) found that of 30 acorns with both *Curculio glandium* Marsham and *Cydia fagiglandana* Z., no acorns germinated. Less than 1 percent of acorns sampled contained more than one species of insect feeding upon a single acorn, while 4 percent contained multiple *Curculio* sp. larvae. The occurrence of multiple infestation of single species within a single nut has been observed for many *Curculio* sp., with numbers as high as eight weevils per acorn occurring in northern California (Swiecki and others 1991). Although not common, this has also been observed in both *Q. engelmannii* and *Q. agrifolia*.

The number of insect-damaged acorns found in this study suggests that insects, mainly *Curculio* sp. weevils and lepidopteran larvae, have the potential to damage high numbers of *Q. agrifolia* and *Q. engelmannii* acorns in southern California. Although the average amount of damage observed on each acorn was minimal, the damage inflicted by these insects and how it may impact subsequent seedling growth is unknown, but potentially significant. Germination tests with damaged acorns are required to determine the impact that insect damage has on seedling growth

Seedling Study

Grasshoppers preferred seedling leaves of *Q. agrifolia* over *Q. engelmannii*. Grasshopper herbivory to live oak seedlings may be a more important limiting factor to their successful regeneration than herbivory to Engelmann oak. *Quercus agrifolia* also may be more susceptible than *Q. engelmannii* to other generalist insect herbivores associated with southern California woodlands.

Quercus agrifolia was preferred over *Q. engelmannii* in the choice test and was a superior host plant as evidenced by greater insect growth in the no-choice tests. When provided with only *Q. engelmannii*, *M. sanguinipes* lost biomass and grew significantly less than animals provided with only *Q. agrifolia*. *Quercus engelmannii* is a poor diet for grasshoppers; its suitability as a host plant for other insect herbivores remains to be documented. The difference in feeding performance and preference may be a result of different chemical compositions in the leaves (Feeny 1970). While previous research has identified chemical composition of *Q. agrifolia* leaves, information about the chemical components in the leaves of *Q. engelmannii* is lacking and further research is needed before a discussion of chemical differences can be applied to the results presented here.

Our results suggest that care should be taken to monitor and/or control grasshoppers in *Q. agrifolia* restoration and replanting areas. This study demonstrated coast live oak to be a relatively adequate food source for a common grasshopper found throughout southern California habitats where current (and future) oak restoration and planting occur. By monitoring the annual population fluctuations of this species, potential damage to newly planted seedlings could be prevented before severe levels of defoliation occur. *Quercus engelmannii*, however, does not appear to provide a sufficient diet for *M. sanguinipes*, suggesting that even with large numbers of grasshoppers, *Q. engelmannii* may receive less grasshopper damage than *Q. agrifolia*.

Coast live oak seedlings have been shown to experience higher mortality than co-occurring species when subjected to simulated herbivory (Muick 1997). Seedlings of *Q. agrifolia* in the Central Valley of California had a reduced survival relative to *Q. douglasii* when subjected to clipping treatments. Following 104 oak seedlings in central coastal California over a 4-year period, White (1966) found an 88 percent survival rate of *Q. douglasii* seedlings, with no *Q. agrifolia* surviving.

In contrast, coast live oak saplings have a much higher success rate with resprouting following herbivory (Griffin 1971, Pillsbury and Joseph 1991); however, acorns or young seedlings, rather than saplings, are usually planted in restoration projects. Because these seedlings are preferred by grasshoppers, herbivory to coast live oak seedlings may greatly impact restoration efforts in southern California.

Given a choice between *Q. engelmannii* and *Q. agrifolia* seedlings in a greenhouse setting, *M. sanguinipes* both preferred and performed better on *Q. agrifolia*. Seedlings of *Q. engelmannii* are apparently not a suitable host for *M. sanguinipes* as evidenced by the loss in biomass resulting during the feeding trials. This suggests that *M. sanguinipes* has the potential to defoliate newly planted *Q. agrifolia* seedlings, but is unlikely to affect *Q. engelmannii*. This study also suggests that greater attention be given to grasshoppers and other invertebrates as potential herbivores in plantings of oak seedlings.

Acknowledgments

This research was completed as partial fulfillment of a Masters' Degree in Entomology, Department of Entomology, University of California, Riverside. Santa Rosa Plateau Ecological Reserve, The Nature Conservancy, Metropolitan Water District, and the University of California, Riverside provided funding. Carole Bell and Zack Principe provided access to SRPER and provided helpful comments. Michael Patten and Jutta Burger provided technical assistance.

References

Adams Jr., T.E.; Sands, P.B.; Weitkamp, W.H.; McDougald, N.K.; Bartolome, J. 1987. **Enemies of white oak regeneration in California.** In: Plumb, T.R.; Pillsbury, N.H., technical coordinators. Proceedings of the symposium on multiple-use management of California's hardwood resources, 1986 November 12-14; San Luis Obispo, CA. Gen. Tech. Rep. PSW-GTR-100. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 459-462.

Adams Jr., T.E.; Sands, P.B.; Weitkamp, W.H.; McDougald, N.K. 1991. **Blue and valley oak seedling establishment on California's hardwood rangelands**. In: Standiford, R.B., technical coordinator. Proceedings of the symposium on oak woodlands and hardwood rangeland management; 1990 October 31-November 2; Davis, CA. Gen. Tech. Rep. PSW-GTR-126. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 41-47.

Andersson, C. 1992. **The effect of weevil and fungal attacks on the germination of *Quercus robur* acorns**. Forest Ecology and Management 50: 247-251.

Arahou, M. 1994. **Biologie et Degats de *Cuculio glandium* Marsham, 1802 (Coleoptera, Curculionidae) et de *Cydia fagiglandana* Zeller, 1841 (Lepidoptera, Tortricidae), deux ravageurs des glands du Chene vert dans le Moyan-Atlas marocain**. L'Entomologiste 50: 253-259.

Bonner, F.T.; Vozzo, J.A. 1987. **Seed biology and technology of *Quercus*.** General Technical Report S-GTR-66. Southern Forest Experiment Station, USDA Forest Service; 1-21.

Borchert, M.I.; Davis, F.W.; Michaelsen, J.; Oyler, L.D. 1989. **Interactions of factors affecting seedling recruitment of blue oak, *Quercus douglasii*, in California (USA).** Ecology 70: 389-404.

Capinera, J.L.; Sechrist, T.S. 1982. **Grasshoppers (Acrididae) of Colorado: Identification, biology and management.** Colorado State University Experiment Station, Fort Collins. Bulletin No. 584S.

Debouzie, D.; Heizmann, A.; Humblot, L. 1993. **A statistical analysis of multiple scales in insect populations: A case study: The chestnut weevil *Curculio elephas*.** Journal of Biological Systems 1: 239-255.

Feeny, P. 1970. **Seasonal Changes in Oak Leaf Tannins and Nutrients as a Cause of Spring Feeding by Winter Moth Caterpillars.** Ecology 51(4): 565-581.

Galford, J.R. 1986. **Primary infestation of sprouting chestnut, red, and white oak acorns by *Valentina glandulella* (Lepidoptera: Blastobasidae).** Entomological News 97: 109-112.

Gibson, L.P. 1969. **Monograph of the genus *Curculio* in the new world (Coleoptera: Curculionidae). part I.** Entomological Society of America Miscellaneous Publications 6: 239-285.

Griffin, J.R. 1971. **Oak regeneration in the upper Carmel Valley.** Ecology 52: 862-868.

Gribko, L.S. 1995. **The effect of acorn insects on the establishment and vigor of northern red oak seedlings in north-central West Virginia.** In: Gottshalk, K.W.; Fosbroke, S.L.C., technical coordinators. Proceedings of the tenth central hardwood forest conference. Morgantown, WV. Gen. Tech. Rep. NE-GTR-197. Forest Service, U.S. Department of Agriculture; 430-441.

Hall, L.M.; George, M.R.; McCreary, D.D.; Adams, T.E. 1992. **Effects of cattle grazing on blue oak seedling damage and survival.** Journal of Rangeland Management 45: 503-506.

Kaushal, B.R.; Pant, M.C; Kalia, S.; Joshi, R; Bora, R. 1993. **Aspects of the biology and control of three species of acorn weevils infesting oak acorns in Kumaun Himalaya.** Journal of Applied Entomology 115: 388-397.

Koenig, W.D.; Knops, J.M.H.; Carmen, W.J. 2002. **Arboreal seed removal and insect damage in three California oaks.** In: Standiford, Richard B.; McCreary, Douglas; Purcell, Kathryn L., technical coordinators. Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. 2001 October 22-25; San Diego, California. Gen. Tech. Rep. PSW-GRT-184. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture [this volume].

Kosrtian, C.F. 1927. **Factors controlling early germination and early survival in oaks.** Yale University School of Forestry Bulletin 19: 1-115.

Larson, 1978. **Effects of late season defoliation and dark periods on initial growth of planted red oak seedlings.** Canadian Journal of Forest Research 8: 97-72.

Lewis, V.R. 1991. **The temporal and spatial distribution of filbert weevil infested acorns in an oak woodland in Marin County.** In: Standiford, R. B., technical coordinator. Proceedings of the symposium on oak woodlands and hardwood rangeland management; 1990 October 31-November 2; Davis, CA. Gen. Tech. Rep. PSW-GTR-126. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 156-160.

Lewis, V.R. 1992. **Within-tree distribution of acorns infested by *Curculio occidentis* (Coleoptera: Curculionidae) and *Cydia latiferreana* (Lepidoptera: Tortricidae) on the coast live oak.** Environmental Entomology 21: 975-982.

Marquis, D.A.; Eckert, P.L.; Roach, B.A. 1976. **Acorn weevils, rodents, and deer all contribute to oak-regeneration difficulties in Pennsylvania.** Res. Paper NE-RP-356. Northern Forest Experiment Station, Forest Service, U.S. Department of Agriculture; 1-5.

McClaran, M.P. 1985. **Regeneration of California blue oak as determined from age structures at multiple bole heights (abstract).** Bulletin of the Ecological Society of America 66: 226.

McCreary, D.D.; Tecklin, J. 1994. **Grasshoppers continue to hamper oak restoration efforts.** Oaks 'N' Folks - A newsletter of the Integrated Hardwood Range Management Program 9, 4-5.

McPherson, G.R. 1993**. Effects of herbivory and herb interference on oak establishment in a semi-arid temperate savanna.** Journal of Vegetation Science 4: 687-692.

Moller, A.P. 1995. **Leaf-mining insects and fluctuating asymmetry in Elm Ulmus glabra leaves.** Journal of Animal Ecology 64: 697-707.

Moller, A.P.; de Lope, F. 1998. **Herbivory affects developmental instability of stone oak, *Quercus rotundifolia***. Oikos 82: 246-252.

Muick, P.C. 1997. **Effects of shade and clipping on coast live and blue oak seedling mortality and growth in California annual grasslands.** In: Pillsbury, N.H.; Verner, J.; Tietje, W.D., technical coordinators. Proceedings of the symposium on oak woodlands: ecology, management, and urban interface issues; 1996 March 19-22; San Luis Obispo, CA. Gen. Tech. Rep. PSW-GTR-160. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 135-145.

Muick, P.C.; Bartolome, J.W. 1986. **Oak regeneration on California's hardwood rangelands.** Transactions of Western Section of the Wildlife Society 22: 121-125.

Oliver, A.D.; Chapin, J.B. 1984. ***Curculio fulvus* (Coleoptera: Curculionidae) and its effects on acorns of live oaks, *Quercus virginiana*.** Environmental Entomology 13: 1507-1510.

Osborne, C.D. 1989. **Early establishment of *Quercus engelmannii* (Fagaceae) on the Santa Rosa Plateau, Riverside County, California.** Loma Linda: Loma Linda University; 98 p. Ph.D. dissertation.

Pavlik, B.M.; Muick, P.C.; Johnson, S.G.; Popper, M. 1991. **Oaks of California.** Cahuma Press and California Oak Foundation. 184 p.

Pillsbury, N.H.; Joseph, J.P. 1991. **Coast live oak thinning study in the central coast of California - fifth-year results.** In: Standiford, R. B., technical coordinator. Proceedings of the symposium on oak woodlands and hardwood rangeland management; 1990 October 31-November 2; Davis, CA. Gen. Tech. Rep. PSW-GTR-126. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 320-332.

Porter, E.E.; Redak, R.A. 1997. **Diet of migratory grasshopper (Orthoptera: Acrididae) in a California native grassland and the effect of prescribed spring burning.** Environmental Entomology 26: 234-240.

Raney, H.G.; Eikenbary, R.D. 1969. **A simplified trap for collecting adult pecan weevils.** Journal of Economic Entomology 62: 722-723.

Scutareanu, P.; Roques, A. 1993. **Insect damage to male catkins female flowers and acorns of *Quercus*-spp in Romania.** Journal of Applied Entomology 115: 321-328.

Shaw, M.W. 1974. **The reproductive characteristics of oak in Britain.** In: Morris; M.G.; Perring, F.H., eds. The British oak, its history and natural history. Faringdon. Botanical Society of the British Isles Conference. Report 14: 162-181.

Steele, M.A.; Knowles, T.; .Bridle, K.; Simms, E.L. 1993. **Tannins and partial consumption of acorns: Implications for dispersal of oaks by seed predators.** American Midland Naturalist 130: 229-238.

Swiecki, T.J.; Bernhardt, E.A.; Arnold, R.A. 1990. **Impacts of diseases and arthropods on California's rangeland oaks.** Prepared for California Department of Forestry and Fire, Forest and Rangeland Resource Assessment Program. Sacramento, CA. 94 p.

Swiecki, T.J.; Bernhardt, E.A.; Arnold, R.A. 1991. **Insect and disease impacts on blue oak acorns and seedlings.** In: Standiford, R.B., technical coordinator. Proceedings of the symposium on oak woodlands and hardwood rangeland management; 1990 October 31-November 2; Davis, CA. Gen. Tech. Rep. PSW-GTR-126. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 149-155.

Swiecki, T.J.; Bernhardt, E.A.; Arnold, R.A. 1997a. **The California oak disease and arthropod (CODA) database.** In: Pillsbury, N.H.; Verner, J.; Tietje, W.D., technical coordinators. Proceedings of the symposium on oak woodlands: ecology, management, and urban interface issues; 1996 March 19-22; San Luis Obispo, CA. Gen. Tech. Rep. PSW-GTR-160. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 543-552.

Swiecki, T.J.; Bernhardt, E.A.; Drake, C. 1997b. **Factors affecting blue oak sapling recruitment.** In: Pillsbury, N.H.; Verner, J.; Tietje, W.D., technical coordinators. Proceedings of the symposium on oak woodlands: ecology, management, and urban interface issues; 1996 March 19-22; San Luis Obispo, CA. Gen. Tech. Rep. PSW-GTR-160. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 157-167.

Tecklin, J.; Connor, J.M.; McCreary, D.D. 1997. **Rehabilitation of a blue oak restoration project.** In: Pillsbury, N.H.; Verner, J.; Tietje, W.D., technical coordinators. Proceedings of the symposium on oak woodlands: ecology, management, and urban interface issues; 1996 March 19-22; San Luis Obispo, CA. Gen. Tech. Rep. PSW-GTR-160. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 267-274.

Tecklin, J.; McCreary, D.D. 1991. **Acorns size as a factor in early seedling growth of blue oaks.** In: Standiford, R.B., technical coordinator. Proceedings of the symposium on oak woodlands and hardwood rangeland management; 1990 October 31-November 2; Davis, CA. Gen. Tech. Rep. PSW-GTR-126. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 48-53.

Walters, R.S.; Auchmoody, L.R. 1993. **Factors limiting northern red oak reproduction in Pennsylvania.** In: Proceedings of the ninth central hardwood forest conference. Gen. Tech. Rep. NC-GTR-161. North Central Research Station, Forest Service, U.S. Department of Agriculture; 271-280.

Weckerly, F.W.; Sugg, D.W.; Semlitsch, R.D. 1989. **Germination success of acorns (*Quercus*): insect predation and tannins.** Canadian Journal of Forest Research 19: 811-815.

White, K.L. 1966. **Old-field succession on Hastings Reservation, California**. Ecology 47: 866-68.